Habitat use by Patagonian toothfish (*Dissostichus eleginoides* Smitt 1898) on the Kerguelen Plateau around Heard Island and the McDonald Islands

by

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ABSTRACT. - The Patagonian toothfish (*Dissostichus eleginoides*) is one of the largest and most ubiquitous benthopelagic predatory fish found in the sub-Antarctic. This species supports the largest single species scalefish fishery in the southern ocean, and the largest fishery for toothfish occurs on the Kerguelen Plateau, with landings of >5 000 t.yr^{-1} from the French EEZ around Kerguelen Islands and 2 500 t.yr^{-1} from the Australian EEZ around Heard Island and the McDonald Islands in 2009. This study provides a synthesis drawn from a range of methods including otolith and tagging analyses, as well as population data collected from fisheries operations and research surveys from across the Kerguelen Plateau, to develop preliminary hypotheses about the Patagonian toothfish lifecycle and the importance of different habitats for different life stage of this species. It is evident that toothfish use a very broad range of habitats across the Kerguelen Plateau throughout their lifespan, from the epipelagic as planktonic larvae and post larvae, to benthopelagic habitats on deep slopes in excess of 2 000 m surrounding sub-Antarctic islands. Toothfish are also capable of making long distance horizontal movements exceeding 2 500 km, and this migration appears to be associated with maturation and movement to one of a few discrete spawning locations in the region. A description of the ecology of the early life history stages, up to 2-3 years old, and the dynamics of spawning stand out as the priority for future research into the biology of this species in this region.

RÉSUMÉ. - Utilisation de l'habitat par la légine australe (*Dissostichus eleginoides* Smitt 1898) sur le Plateau de Kerguelen autour des îles Kerguelen et McDonald.

La légine australe (*Dissostichus eleginoides*) est un des poissons prédateur bentho-pélagique les plus grands et les plus ubiquistes que l'on puisse trouver dans le sub-antarctique. Cette espèce est l'objet de la plus importante mono-pêcherie de l'océan Austral et la pêcherie la plus conséquente de cette espèce est située sur le Plateau de Kerguelen. Les débarquements y atteignaient, en 2009, plus de 5 000 t annuellement pour la ZEE française des îles Kerguelen et 2 500 t pour la ZEE australienne des îles Heard et McDonald. A partir d'une gamme de méthodes comprenant les analyses sur les otolithes et le marquage, des données issues des opérations de pêche et des campagnes de recherche sur le Plateau de Kerguelen, il est possible d'établir un schéma général permettant d'avancer des hypothèses préliminaires sur le cycle vital de la légine australe et sur l'importance des différents habitats occupés lors des différents stades de développement. Il apparaît que la légine australe utilise un vaste domaine d'habitats sur le Plateau de Kerguelen au cours de son cycle vital, du domaine épipélagique lors de ses stades larvaire et post-larvaire planctoniques aux habitats benthopélagiques sur les pentes profondes entourant ces îles sub-antarctiques au-delà de 2 000 m de profondeur. La légine australe est aussi capable d'effectuer des mouvements horizontaux sur de longues distances, excédant parfois 2 500 km, et cette migration semble liée à la maturation et au mouvement vers une ou plusieurs frayères peu connues dans la région. La description de l'écologie des stages précoces, jusqu'à deux ou trois ans, et la dynamique de la reproduction semblent les priorités des prochaines recherches sur la biologie de l'espèce dans cette région.

Key words. - Kerguelen Plateau - Heard Island - Southern Ocean - *Dissostichus eleginoides*.

The nototheniid genus *Dissostichus* contains two species, the Antarctic toothfish, *D. mawsoni* Norman 1937 and the Patagonian toothfish, *D. eleginoides* Smitt 1898. The Antarctic toothfish is primarily confined to waters south of 60°S, while the Patagonian toothfish has a broad distribution, having been recorded from around all sub-Antarctic islands, and extending as far north as 20°S along the west coast of South America (e.g., Gon and Heemstra, 1990; Eastman, 1993; Arkhipkin *et al*., 2003).

At the scale of ocean basins, highly significant genetic differences have been found between Patagonian toothfish, with fish collected at Macquarie Island, on the Kerguelen Plateau around Heard Island and the McDonald Islands (HIMI), South Georgia/Shag Rocks, and the Patagonian shelf, all

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showing significantly different mitochondrial DNA random fragment length polymorphisms (RFLPs) (Appleyard *et al.*, 2002; Shaw *et al.*, 2004). At smaller scales, genetic studies show homogeneity in mtDNA RFLPs between populations of toothfish sampled around islands in the Indian Ocean sector of the Southern Ocean, including HIMI, Kerguelen, Crozet and Prince Edward and Marion Islands (Appleyard *et al.*, 2004). Based on these results, individuals from the populations around the islands in the western Indian Ocean sector of the southern ocean are likely to interbreed on occasion, while genetic exchange across deep ocean troughs and basins is unlikely to have occurred for millennia. A metapopulation of toothfish in the southern Indian Ocean is further supported by the results of recapture tag studies conducted on the Kerguelen Plateau, which indicate that the majority of toothfish recaptured do not move large distances from year to year, but can occasionally move upwards 2 500 km, from the plateau around HIMI to north of Crozet Islands (Williams and Lamb, 2002; Williams *et al.*, 2003; Welsford *et al.*, 2007).

Since the 1990s, Patagonian toothfish have dominated removals of finfish from the sub-Antarctic, including the area managed under the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). The largest fisheries for Patagonian toothfish are centered in the Atlantic Sector of the Southern Ocean, around South Georgia and the Patagonian shelf, and this is where the fishery targeting this species began (Kock, 1992). However the Indian Ocean Sector of the Southern Ocean, particularly on the Kerguelen Plateau, is also a very important area for this species and significant fisheries target it in this region. For example, in the 2007-2008 fishing season, approximately 20 200 t of *Dissostichus* spp. are estimated to have been captured globally; of these, around 4 000 t are likely to have been Antarctic toothfish, and of the remainder Patagonian toothfish, almost 38% was captured in Statistical Divisions 58.5.1 and 58.5.2 of the CCAMLR area, which cover the French and Australian Exclusive Economic Zones (EEZs) around Kerguelen Islands and HIMI (CCAMLR, 2010). Therefore, the populations on the Kerguelen Plateau constitute the most significant centre of abundance of toothfish outside of the South Atlantic sector.

Extensive trawling was conducted by vessels of the former Soviet Union and Poland across the Kerguelen Plateau, including around HIMI during the 1970s. These vessels primarily targeted mackerel icefish (*Champsocephalus gunnari* Lönnberg 1905) and grey and marbled rock cods (*Lepidonotothen squamifrons* (Günther 1880) and *Notothenia rossii* Richardson 1844). These vessels fished on the shallow plateau and banks of the region and small by-catches of juvenile toothfish were common around Kerguelen Islands (Duhamel and Hureau, 1985).

France declared a 200 nm EEZ around Kerguelen Islands in 1978, and regulation of fishing commenced immediately thereafter. Details of the fisheries in the French EEZ are described in detail in Duhamel *et al.* (2011, this volume). Australia also declared a 200 nm Australian Fishing Zone (AFZ) around HIMI in 1979.

On the plateau of the Australian zone (Fig. 1), no commercial fishing occurred after the declaration of the AFZ throughout the 1980s. Research fishing to determine the status of fish stocks was conducted by a Soviet research vessel, the FRV *Professor Mesyatsev* in 1987, but did not catch substantial amounts of toothfish (Gerasimchook *et al.*, 1988). The Australian research vessel RV *Aurora Australis* conducted three trawl surveys across the plateau in 1990, 1992 and 1993, leading to the first estimate of abundance and sustainable yields of toothfish (Williams and de la Mare, 1995).

Commercial fishing by Australian vessels then commenced in 1997 when two Australian trawlers began targeting Patagonian toothfish and mackerel icefish on the south-eastern part of the plateau, fishing down to 1 000 m. Demersal longlining commenced in 2003, and trials of pots have also been conducted in 2006 and 2009-2010. These latter vessels can successfully catch toothfish to depths in excess of 2 500 m, therefore providing a window on the toothfish population across a very broad range of depths.

Studies of toothfish populations in other regions have shown that toothfish are not randomly distributed. Around South Georgia and on the Falklands shelf in the South Atlantic sector (Agnew *et al.*, 1999; Arkhipkin *et al.*, 2003; Arkhipkin and Laptikhovsky, 2010), and in the Indian Ocean sector around Kerguelen Islands and on the Del Cano Rise (Duhamel, 1987; Duhamel, 1993; López Abellán, 2005), toothfish length is strongly correlated with increasing depth. At South Georgia, Agnew *et al.* (1999) also found larger, mature female toothfish deeper on the slope, and smaller, mature male toothfish on the shallower slopes, with both sexes converging in intermediate depths to spawn. Lord *et al.* (2006) found sex ratios were biased towards males on the western side of the Kerguelen Islands, particularly on Skif Bank, which is a known spawning area. Therefore, toothfish apparently exhibit responses to both bathymetry and regional topography; however such patterns have not been investigated in detail around HIMI.

This study seeks to review the data collected by commercial and research fishing on toothfish from the Australian EEZ at HIMI, and from other studies in the region to further develop hypotheses regarding the use of habitats by different life stages of Patagonian toothfish across the Kerguelen Plateau. Such hypotheses can then be used to inform management strategies for fisheries targeting toothfish in the region; for example, to assist in ensuring that management takes into account the spatial scales over which the toothfish stock

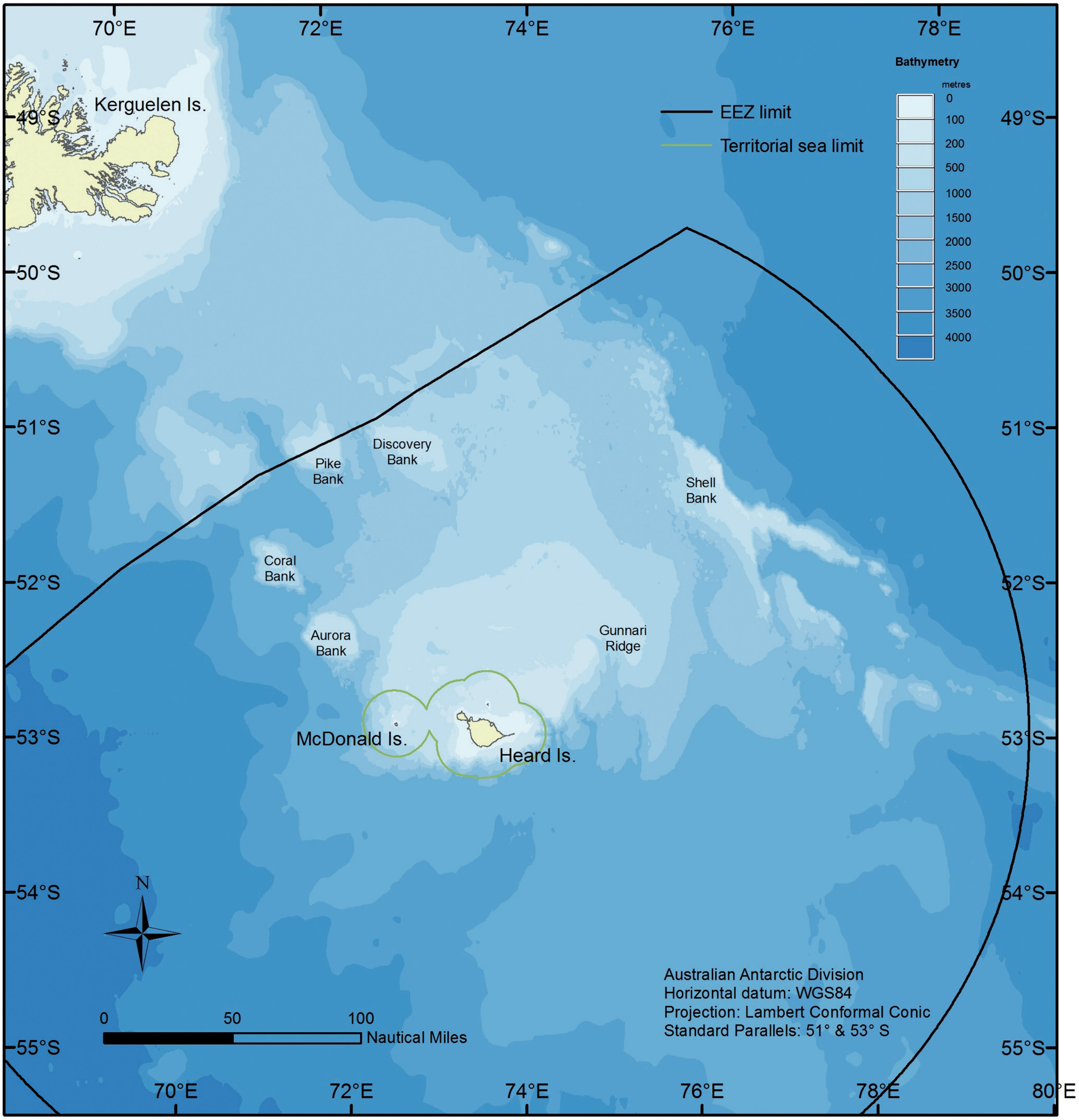

Figure 1. - Map of the Australian Territory of Heard Island and the McDonald Islands, and the surrounding portion of the Kerguelen Plateau, where the commercial fishery for Patagonian toothfish (*Dissostichus eleginoides*) fishery occurs, and the data for this study is drawn.

and fishery may extend, and the timing and duration of key events in the lifecycle, as well as informing models of the ecosystem of the Kerguelen region in which the behaviour of toothfish as predators and prey species varies at different times and locations.

MATERIALS AND METHODS

Data sources

Data for this study are primarily drawn for activities conducted by Australian fishing and research vessels, operating

Table I. - Numbers of observations of length and age of Patagonian toothfish (*Dissostichus eleginoides*) by year and fishing gear type, caught in the Australian EEZ at Heard Island and the McDonald Islands. Numbers of fish aged are shown in brackets.

Year	Gear Type			Total
	Trawl	Longline	Pot	
1990	363 (-)			363 (-)
1992	246 (-)			246 (-)
1993	179 (-)	11 (-)		190 (-)
1997	9 229 (12)			9 229 (12)
1998	14 203(288)			14 203(288)
1999	15 752 (547)			15 752(547)
2000	21 732 (767)			21 732 (767)
2001	30 467 (803)			30467 (803)
2002	21 227 (834)			21 227 (834)
2003	27 373 (533)	4 194 (181)		31 567 (714)
2004	20 026 (302)	14 363 (2)		34 389 (304)
2005	19 596 (351)	13 138 (20)	539 (-)	33 273 (371)
2006	17 291 (640)	9 897 (406)	5 355 (170)	32 543 (1216)
2007	16 151 (778)	8 785 (375)		24 936 (1153)
2008	16 488 (718)	16 597 (40)	9 (-)	33 094 (758)
2009	15 242 (643)	30 497 (-)	773 (-)	46 512 (643)
2010	10 578 (438)	16 916 (-)		27 494 (438)
Total	114 398 (7 654)	256 143 (1 024)	6 676 (170)	377 217 (8 848)

Table II. - Numbers of recaptured Patagonian toothfish (*Dissostichus eleginoides*) released within the Australian EEZ at Heard Island and the McDonald Islands by year, location and method of recapture, including recaptures from the French EEZ around Kerguelen Islands and Crozet. Numbers of fish aged are shown in brackets.

Year	Australian EEZ		French EEZ	Total
	Trawl	Longline	Longline	
1998	98 (62)			98 (62)
1999	108 (63)			108 (63)
2000	192 (92)			192 (92)
2001	302 (123)			305 (206)
2002	394 (206)		3	398 (238)
2003	413 (238)	1	7	421 (238)
2004	377 (270)	5 (2)	5	387 (272)
2005	404 (225)	23 (20)	8	435 (245)
2006	300 (119)	21 (26)	17	338 (145)
2007	309 (100)	29 (40)	17	355 (140)
2008	173 (65)	59 (42)	17	249 (107)
2009	152	75	22	249
2010	67	77	17	161
Total	3 289 (1563)	290 (130)	117	3 696 (1693)

in the Australian EEZ around HIMI between 1997 and 2010. Each year, since the commencement of the toothfish fishery in the Australian EEZ, a Random Stratified Trawl Survey (RSTS) has been conducted by a commercial trawl fishing vessel across the plateau. Typically, more than 150 survey stations are completed, covering all waters down to 1 000 m, including those inside the HIMI Marine Reserve (Welsford *et al*., 2006). Comprehensive data is collected on the abundance, size and biology of demersal fishes caught, including toothfish. All fishing vessels also carry two scientific observers, who independently collect catch and effort data, as well as collecting data on catch and bycatch species. As a consequence, we have access to a large number of individual observations of toothfish around HIMI. Observers also routinely collect otoliths from toothfish. Recent studies have shown that these otoliths can be reliably processed to produce age estimates (e.g., Welsford *et al*., 2009) and a large number of these fish have been aged (Tab. I).

Since 1998, scientific observers have also tagged toothfish for each season. To date, over 21 800 toothfish have been tagged and released and 3 696 have been recaptured. The majority of these fish are recaptured adjacent to where they were released; however, increasing numbers are being reported from the toothfish fishery around Kerguelen Islands. Each record includes time and location of release and recapture, as well as the size of the animal when released and its size and sometimes its sex at recapture, and a large number of these recaptures have also been aged (Tab. II).

Analyses

We modelled the relationships between sex ratio, age and size of toothfish, gear type, capture location, depth, month, year and catch rate using generalised additive models (GAMs, implemented in R (R Development Core Team, 2010) using the *gam()* function in the *mgcv* package (Wood, 2006). This is to test the null hypothesis that male and female toothfish, of all sizes, are randomly distributed in catches across the plateau around HIMI. Similarly, we modelled the relationships between sex, size and age at release, and recapture and release location, movement rate, movement direction and movement distance using generalised additive models to test the null hypothesis that movement of tagged toothfish is random in the region.

Datasets were quality checked to remove samples where numbers of fish measured or sexed were low (< 5 individuals), or measurements were missing or flagged as uncertain. As distinguishing sex in small juvenile toothfish can be difficult, samples of fish smaller than 400 mm were removed for the purposes of calculating sex ratios within samples. Because potting has only been used sporadically to date, and longlining has only occurred since 2003, data collected from pots, and prior to 2003 was excluded from the GAMs where gear type was determined to be a significant factor.

A comprehensive model was then constructed including all available variables in the first instance, with splines fitted to continuous variables (e.g., depth, length, latitude and

Table III. - Results of an analysis of variance for the generalised additive model of mean length of Patagonian toothfish (*Dissostichus eleginoides*) captured in the Australian EEZ at Heard Island and the McDonald Islands by longline and trawls, 2003-2010. Note that parametric terms have a *t* statistic and smooth terms have an *F* statistic estimated, as indicated in the *t*, *F* column. All terms are highly significant at the $p < 0.05$ level.

Term	Factor	df	*t* ,*F*	*p*	n	R^2
Parametric	Intercept		252.6	< 0.001	15 165	0.761
	Gear	1	-25.1	< 0.001		
	Sex	1	-36.83	< 0.001		
Smooth	Depth	8.2	133.9	< 0.001		
	Year	5	540.8	< 0.001		
	Longitude, latitude	19	371.3	< 0.001		

longitude). Models fitted to sex ratio data were modelled with a binomial error distribution with a logit link function, and length data was modelled with a Gamma error distribution and a log link function. The most parsimonious model was selected by progressively removing terms to achieve the model with the minimum value of Akaike's Information Criterion (AIC) (Akaike, 1974). The change in the R^2 value and deviance explained for each model was also considered as an indication of the quality of fit.

RESULTS

Size distribution

Data was available for size classes of fish from 25 cm up to 175 cm. Only two records of fish less than 20 cm where found, captured on Shell Bank (see Fig. 1). Very little fishing has occurred on Shell Bank in recent years, as most of it falls inside the HIMI Marine reserve, and is not typically surveyed during the annual RSTS.

A highly significant relationship between mean length of fish in a sample and depth, year, gear type, latitude, longitude and sex was estimated by the most parsimonious GAM (Tab. III). Month was also significant, but the AIC value indicated that this term did not significantly improve the model fit to the data, and so was excluded. Figure 2 shows that longlines tend to catch fish more than 10 cm larger than trawls in similar locations. There has been a decline in the mean size of fish, from near 83 cm in 2003, down to 75 cm in 2007 and stable up to 2010. Females also tend to be more than 4 cm larger than males in the same sample.

Depth and the latitude and longitude of fishing had the largest effect on the mean length toothfish captured. When the effect due to depth was isolated, predicted mean length

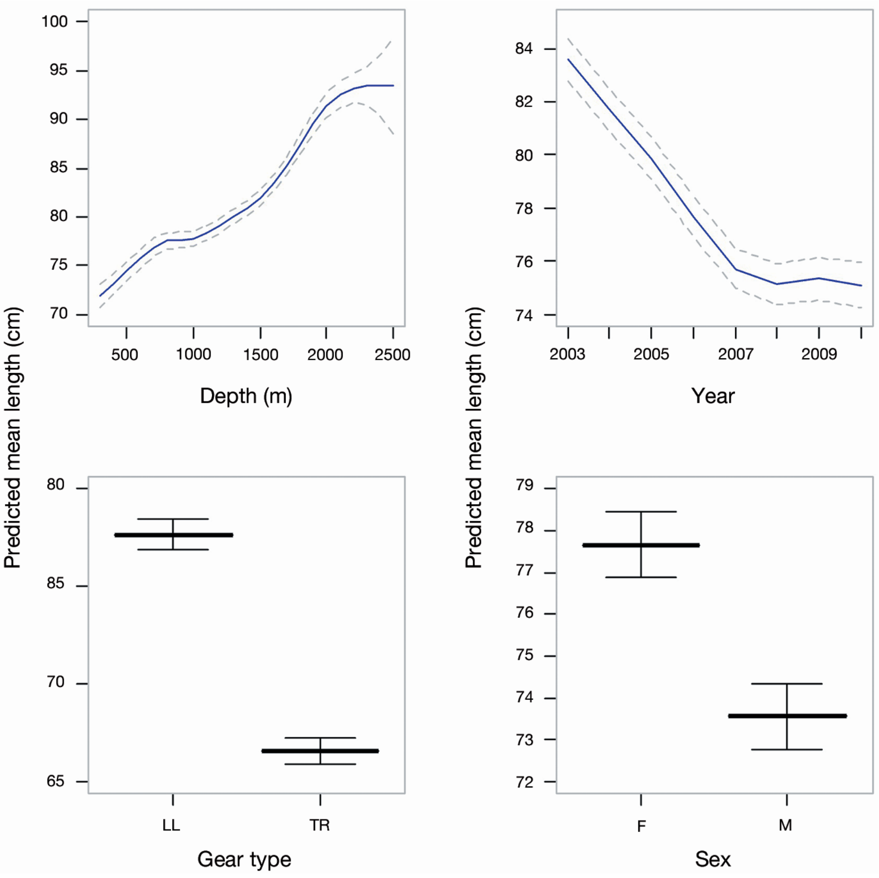

Figure 2. - Prediction from a generalised additive model of mean total length of Patagonian toothfish (*Dissostichus eleginoides*) captured in the Australian EEZ at Heard Island and the McDonald Islands by longline (LL) and trawls (TR), 2003-2010. Plots show the predicted mean length where all other variables are held fixed at a representative value. For example, the top left panel shows the predicted relationship between depth and mean length of females in 2006, at 75°E 54°S, captured by longline. Depth was fixed at 900 m for the other plots. Dotted lines and error bars are 95% confidence intervals.

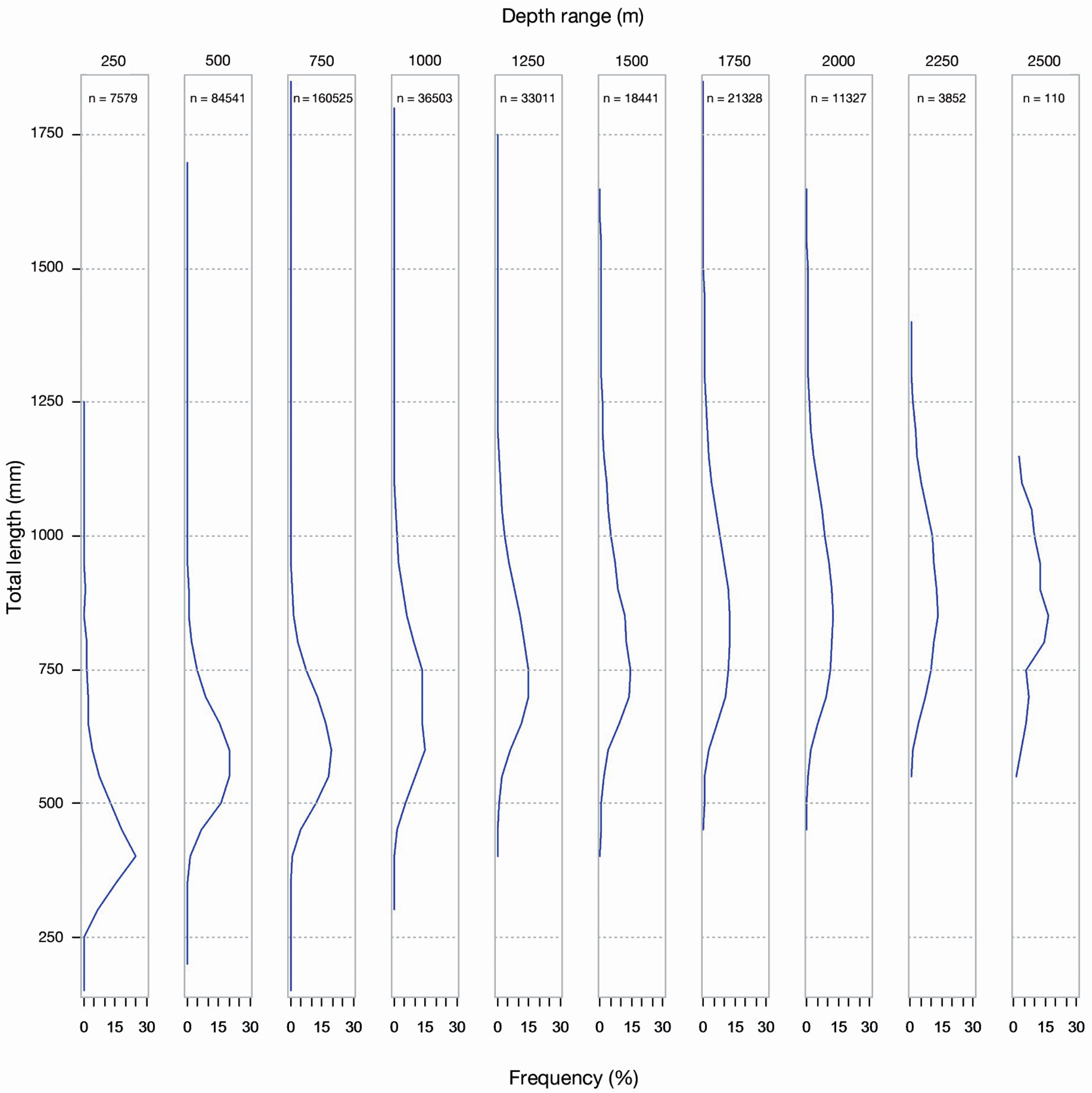

Figure 3. - Catch weighted length frequency of Patagonian toothfish (*Dissostichus eleginoides*) captured in the Australian EEZ at Heard Island and the McDonald Islands, pooled across gear types and years 1997-2010.

increased steadily from around 72 cm in 400 m depth to around 93 cm for depth in excess of 2000 m. This trend is also evident in the catch weighted length frequencies, pooled across years and gears (Fig. 3), with the modal size increasing with increasing depth.

However, due to the topography of the plateau in the region, there is a complex relationship between depth and latitude and longitude, as shown in the upper panel of figure 4 and therefore any depth effect will be confounded to a degree with the effect attributed to latitude and longitude. When mean length is predicted on the basis of location and the mean fishing depth recorded at that location (shown in the lower panel of figure 4), it is evident that the relationship between mean length, depth and location is more complex than simply larger fish being found in deeper areas; for example, samples of the smallest fish (mean length < 50 cm) seem to be focused in an area roughly corresponding to Gunnari Ridge, rather than the shallowest areas around Heard Island itself. Further, larger fish are not restricted to the slope areas, with a mean length greater than 70 cm being predicted for the north-western part of the plateau in relatively shallow depths.

Sex ratio

The most parsimonious GAM indicated highly significant relationships between sex ratio of toothfish captured

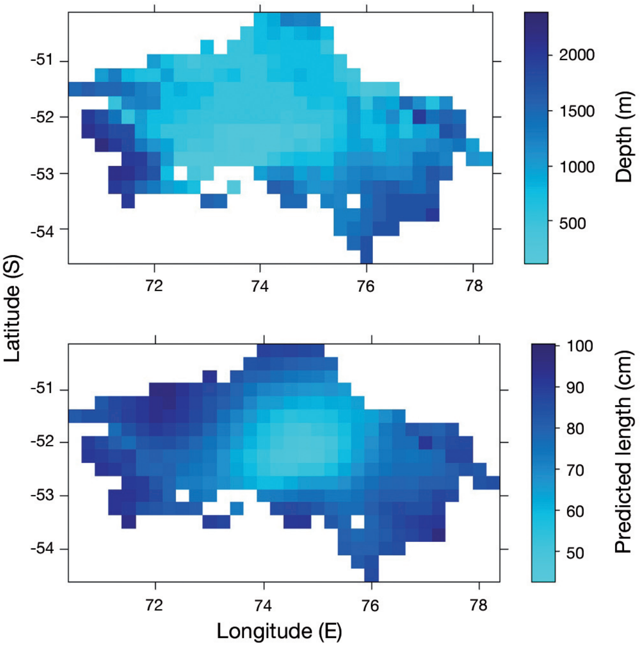

Figure 4. - Mean fishing depth (top panel), and predicted mean total length from a generalised additive model of female Patagonian toothfish (*Dissostichus eleginoides*) caught by longline in 2006 in the Australian EEZ at Heard Island and the McDonald Islands (bottom panel). Mean lengths are predicted across the grid of latitude and longitude and the mean fishing depth reported for that grid square.

Table IV. - Results of an analysis of variance for the generalised additive model of sex ratio of Patagonian toothfish (*Dissostichus eleginoides*) captured in the Australian EEZ at Heard Island and the McDonald Islands by longline and trawls, 2003-2010. All terms are highly significant at the $p < 0.05$ level.

Factor	df	χ^2	p	n	R^2
Depth	4.86	335	< 0.001	21 983	0.912
Length class	8.94	5031	< 0.001		
Year	1.00	129	< 0.001		
Longitude	9.96	352	< 0.001		

and length class, depth fished, year, gear type and longitude (Tab. IV). Month and latitude were also significant at the $p < 0.05$ level, however the AIC value for these models indicated the benefit in model fit of their inclusion was negligible, contributing less than 0.01% improvement to R^2. Figure 5 shows that length class has the greatest effect on the predicted sex ratio, being strongly biased towards females for all sizes above 70 cm, and males being absent from the population of fish greater than 140 cm. A strong effect due to longitude is also evident, with sample from the eastern part of the plateau being ~55% females when all other variables are fixed, while samples from west of 73°E being strongly male dominated. A significant increase in the proportions of females over the years 2003-2010, and an overall decrease with depth was predicted by the model; however, the scale

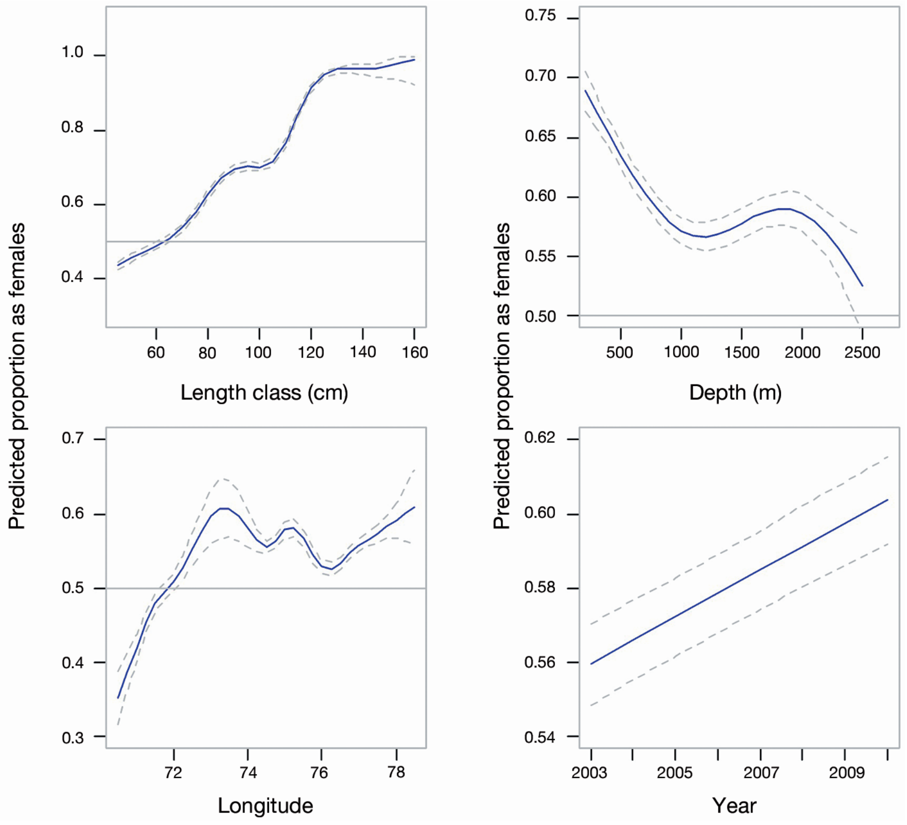

Figure 5. - Prediction from the generalised additive model of sex ratio of Patagonian toothfish (*Dissostichus eleginoides*) captured in the Australian EEZ at Heard Island and the McDonald Islands by longline and trawls, 2003-2010. Plots show the predicted sex ratio where all other variables are held fixed at a representative value. For example, the top left panel shows the predicted sex ratio by length class in 2006, at a depth of 900 m, at 75°E, captured by longline. Length was fixed at 75cm for the other plots. Dotted lines are 95% confidence intervals. 1:1 sex ratio is indicated by the horizontal grey line in each plot.

of these effects was minor compared to the effect of size and longitude.

Age Distribution

Length at age data for all fish analysed from the region is shown in figure 6. From this plot, it is evident that females dominate in the older and larger classes, with males longer than 100 cm or older than 17 years uncommon, while females up to 35 years old and over 170 cm have been recorded.

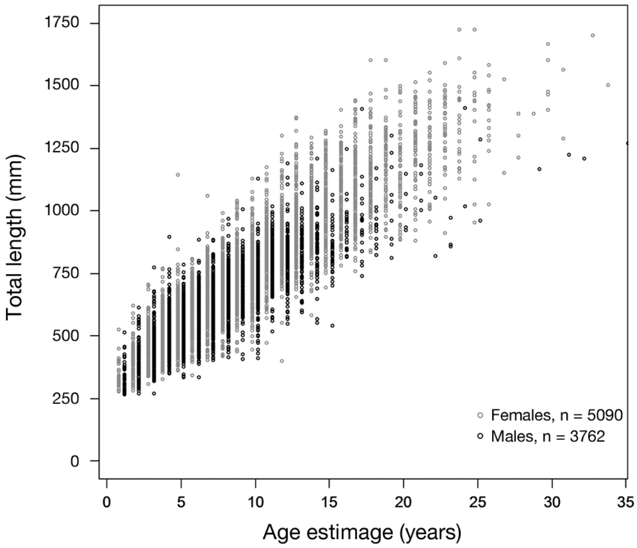

Figure 6. - Estimated age and total length for male and female Patagonian toothfish (*Dissostichus eleginoides*) from the Australian EEZ at Heard Island and the McDonald Islands. Data includes individuals aged from research and commercial samples from 1990-2010.

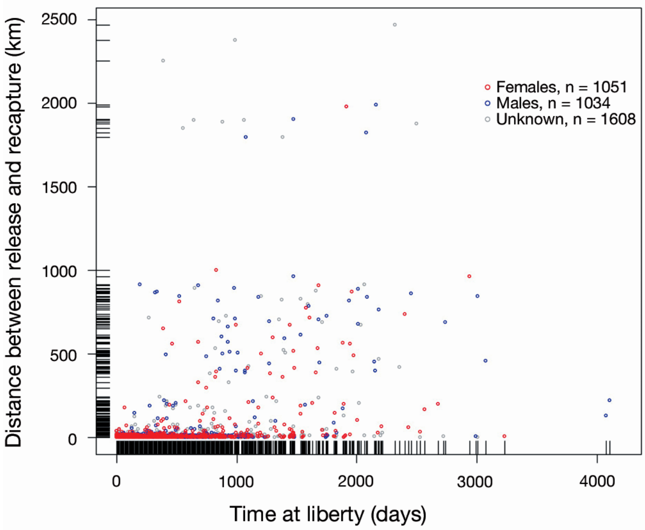

Figure 7. - Distance moved by time at liberty for Patagonian toothfish (*Dissostichus eleginoides)* released in the Australian EEZ at Heard Island and the McDonald Islands, between 1998 and 2010.

Movement of tagged fish

The overwhelming majority of toothfish tagged and recaptured at HIMI are recovered < 50 km distance from where they were released (Fig. 7). There is no clear relationship between time at liberty and distance moved, with many fish being recaptured less than 100 km from where they were released, up to ~1 000 days after they were first tagged, while other animals have travelled at least 2 000 km during the same period. Recaptures also decline rapidly after ~1 000 days at liberty, indicating that tagged fish remain most vulnerable to recapture during this interval. The majority of fishing and tagging effort has been focused on a few areas, where trawling effort and catches were most concentrated, and as a result more than 70% of fish were released within 25 km of the centre of the main trawl ground (ground b, *sensu* Candy and Constable, 2008) (Fig. 8), hence the relatively small number of fish recaptured that have moved large distances is also likely to be influenced by the decreased likelihood of being captured if they move out of an area of focused fishing activity.

The small number of very long travel distances recorded all come from fish that were recaptured by long-liners in the French EEZ around Kerguelen Islands and Crozet to the northwest. This is evident in figure 9, where the largest distances travelled tend to have bearings between 265° and 355°, approximately parallel to the main axis of the Kerguelen Plateau.

Attempts to develop GAMs to predict distance or direction travelled based on a range of covariates produced mod-

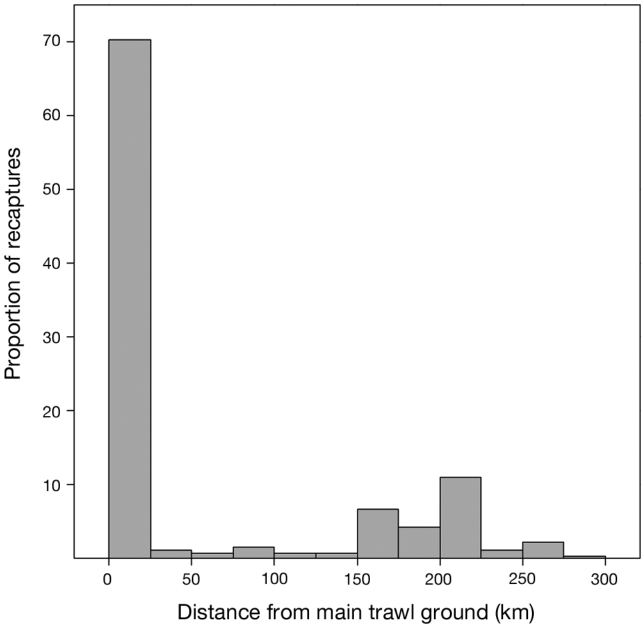

Figure 8. - Distribution of the distance of the release location from the main trawl ground of Patagonian toothfish (*Dissostichus eleginoides)* tagged and released in the Australian EEZ at Heard Island and the McDonald Islands, between 1998 and 2010.

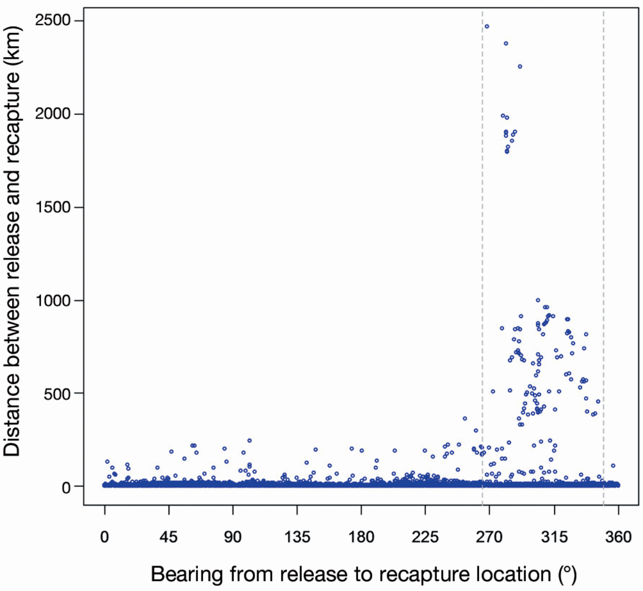

Figure 9. - Distance moved by bearing from the release to the recapture location (0/360° corresponding to north) for Patagonian toothfish (*Dissostichus eleginoides)* released in the Australian EEZ at Heard Island and the McDonald Islands, between 1998 and 2010. Dotted reference lines bracket the bearings of all tag recaptures that moved from the Australian EEZ to the French EEZs around Kerguelen Islands (> 500 km) and Crozet Islands (>1 700 km).

els with poor fits to the data, and are not shown. Graphically, it is evident that length and sex may have been factors in the distance and rate of movement, with males tending to make up a slightly larger proportion of those fish recaptured more than 500 km from where they were released, while fish that moved longer distances tended to be primarily between 45 and 90 cm in length (Fig. 10).

DISCUSSION

This study reinforces the conclusions of previous work on Patagonian toothfish in the Indian Ocean and other areas, revealing complex relationships between this species and the seascape.

For example, other studies have shown the tendency for larger toothfish to move into deeper waters where they grow (Agnew *et al.*, 1999; Arkhipkin *et al.*, 2003; Arkhipkin and Laptikhovsky, 2010). This trend is also shown in this study for fish at HIMI, with the smallest size classes (~30 cm) of fish encountered in the Gunnari Ridge area (see Fig. 1), and the largest on the deeper slopes to the west and east of the plateau. Why such a relationship should exist across the range of this species is not clear, however, it may be related

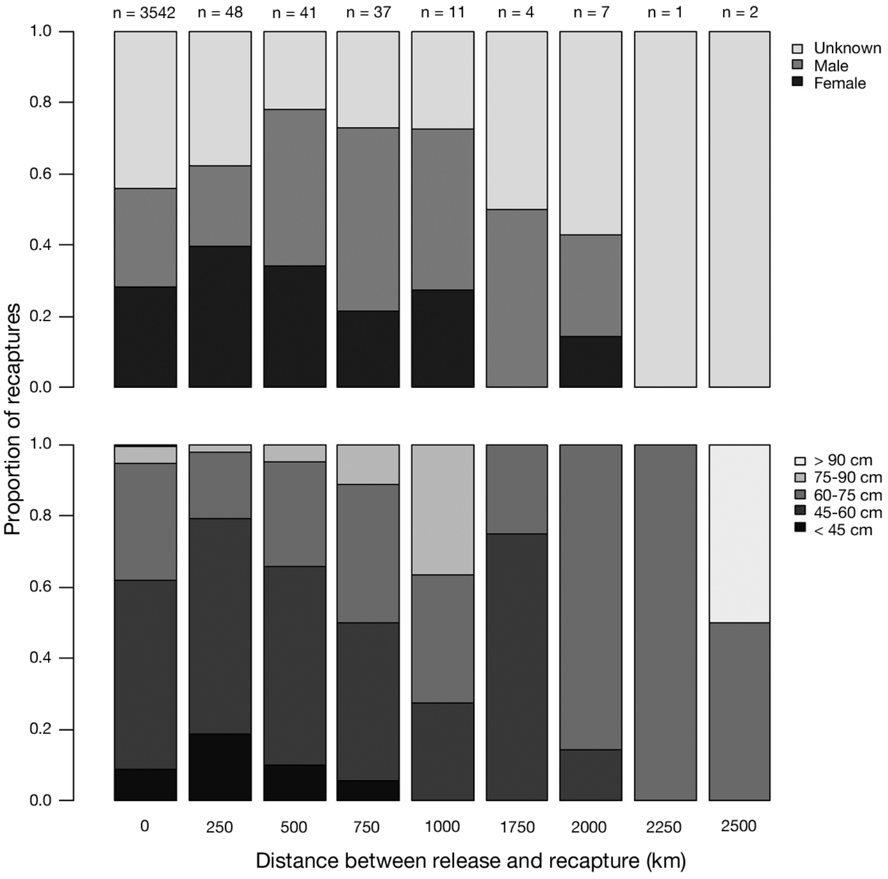

Figure 10. - Movement distances of tagged Patagonian toothfish (*Dissostichus eleginoides)* released in the Australian EEZ at Heard Island and the McDonald Islands, by sex (top panel) and length class (bottom panel), for all recaptures between 1998 and 2010.

to larger fish moving to deeper areas, where availability of larger fish prey such as grenadiers increases, or pressures such as cannibalism leading to habitat partitioning between size classes of fish.

However, the analysis in this study reveals that this relationship can be modified around seabed features such as Pike Bank, which stands out as an area where much larger fish are encountered than are found in other areas of equivalent depth on the plateau. Recent studies of benthic assemblages in the region indicate that Pike Bank has unusually high biomass of habitat forming organisms such as sponges, relative to other areas of the shallow plateau, which may provide attractive foraging opportunities for larger fish.

Larger fish being encountered by longline than trawl is likely to reflect the fact that trawling tends to select smaller or younger fish than longline (Candy and Constable, 2008). The mean size of males in the sample was found to be smaller than females, and may reflect the differential growth of the two sexes, with animals of similar age co-occurring in samples. The effect, however, is small, and may not be of biological significance.

The results of the analysis of covariates of sex ratio, and length at age indicate that males and females show important differences in their distribution and biology. The relationship between sex ratio and length is likely to be a product of the absence of large males in catches at HIMI. The small increase in the proportion of females between 2003 and 2010 may be due to the increase in proportion of catch taken by longline, and hence the proportion of larger individuals has increased over the same period (SC-CAMLR, 2009). However, the tendency for more males to be found on the western side of the plateau than on the eastern side or the plateau itself, and the rarity of males above 100 cm requires further explanation.

The situation at HIMI contrasts with the pattern described in the French EEZ around Kerguelen Islands, where sex ratios are even, with the exception of being strongly biased towards males on Skif Bank, a known spawning location west of Kerguelen Islands (Lord *et al*., 2006). Furthermore, in the Kerguelen population, males apparently do not reach as large a size as females, but older males (in excess of 30 years) seem to be present in catches in similar numbers to females (Ashford *et al*., 2005).

Analysis of the movement of tagged fish reinforces the conclusions of recent reviews of tag recapture data in the region (Williams *et al*., 2003; Welsford *et al*., 2007), that

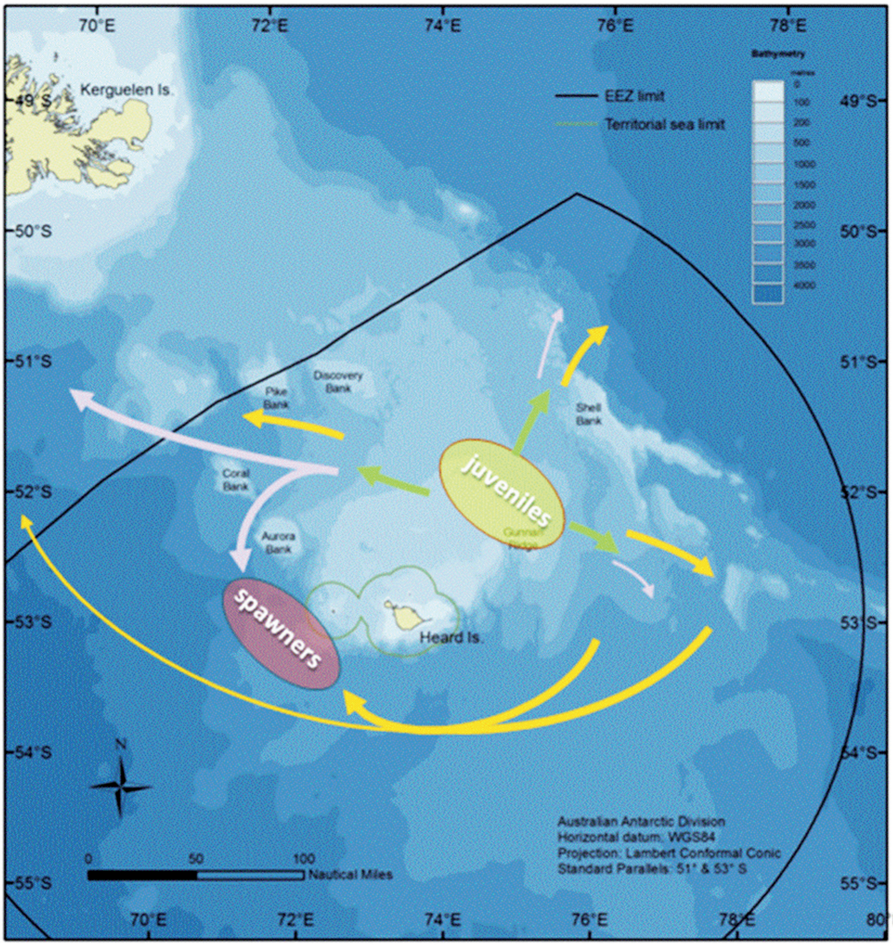

Figure 11. - Schematic of hypothetical movements of Patagonian toothfish (*Dissostichus eleginoides*) in the Australian EEZ at Heard Island and the McDonald Islands. Juveniles settle on the shallow plateau, and move out into deeper areas from the shallow plateau (green arrows). As they mature, females continue to move to the deeper slopes around the plateau (yellow arrows), while most males start to move to the north and west (purple arrows), with some fish crossing into the French EEZ around Kerguelen and Crozet Islands. This differential movement by sex, combined with males maturing at a younger age and smaller size leading to a female-biased sex ratio that is most pronounced to the east, and least pronounced in the west, in the vicinity of the recently discovered spawning locations on the deep slope west of Heard Island, and would also contribute to the rarity of large males (> 100 cm) in the Australian EEZ.

although many of the toothfish recaptured travel short distances, some toothfish are making very long journeys, leaving the Australian EEZ to be recaptured in the French commercial fishery to the NW. Unfortunately, many of these recaptures are unable to be sexed, however there is some evidence that male toothfish are more likely to make the large movements that results in them being recaptured in the French EEZ to the NW.

We propose the following hypothesis that goes some way to combining these observations (Fig. 11). Juvenile toothfish settle on the shallow regions across the plateau, aggregating in the SE of the plateau by the time they reach around 30 cm, and become vulnerable to the trawl fishery. As they grow, they migrate deeper and then leave the plateau and the main trawl ground and become vulnerable to the longline fishery as they move onto the deeper slopes. As they approach maturity (Lord *et al*. (2006) estimated 50% maturity being at around 70 cm for males and 90 cm for females, based on data from the Kerguelen fishery), fish begin to move towards the spawning grounds on the western side of the plateau, with the males tending to move further, subsequently moving along the slope into the French EEZ, and across to Crozet Island, leading to a relative deficit of males in the HIMI EEZ. The generally larger/older females and smaller /younger mature males then spawn at locations such as Skif Bank and the western slopes of the HIMI plateau where spawning activity has been recently discovered (AAD, unpublished data).

There are still significant uncertainties with respect to toothfish behaviour and habitat use throughout their lives which remain to be resolved. The dynamics of the recently discovered spawning location in the Australian EEZ is unknown. The exact path they use to move, for example, from the shallow plateau near HIMI across abyssal depths to Crozet Islands, and also why such long distance migrations may have evolved, is also worthy of further investigation. Travelling to the west of the plateau before spawning may serve to enhance egg and larval retention over the plateau in a prevailing west to east water flow. However, as the eggs and larvae of toothfish are very rarely encountered, this constitutes an important area of future enquiry.

It is evident that toothfish have a complex lifecycle, and as they pass through different life stages, over possibly 30 or more years of life, they may move great distances and occupy the broadest range of depths of any sub-Antarctic species. These insights will be critical for informing current and future management of this species across the Kerguelen Plateau. The data being collected from fishing and research vessels in the region constitutes a very powerful tool for understanding this species, and combining the data available from the French and Australian EEZs will no doubt enable considerable further refinement of current models of species and ecosystems in the region.

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